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CYTOGENETIC DATA ON THE RODENT FAMILY GERBILLIDAE

MAZIN B. QUMSIYEH AND DUANE A. SCHLITTER

Gerbils and jirds comprise 16 genera with between 86 and 90 species (Nowak and Paradiso, 1983; Carleton and Musser, 1984). The group is unique and probably represents a separate family of rodents—the Gerbillidae (Heptner, 1933; Chaline *et al.*, 1977; Carleton and Musser, 1984; Qumsiyeh, 1986*a*). Recent morphologic, karyotypic, and electrophoretic studies have documented an accelerated rate of evolution and diversification in several lineages within this economically and medically important group of rodents (Benazzou *et al.*, 1982*a*, 1982*b*, 1984; Pavlinov, 1982; Qumsiyeh, 1986*b*; 1989; Qumsiyeh *et al.*, 1987; Qumsiyeh and Chesser, 1988).

Jotterand-Bellomo (1984) summarized diploid and fundamental numbers for rodents including 42 species of Gerbillidae. Herein, we provide a more complete and detailed account and updated information on chromosomes of gerbils and jirds. This includes a review of 1) known diploid numbers and autosome and sex chromosome morphology, 2) heterochromatin evolution, 3) individual and geographic variation, and 4) meiotic studies. We hope this review will serve as a resource and thereby stimulate additional research on the evolutionary relationships of gerbils.

Interspecific chromosomal variation.—Karyotypic data from nondifferentially stained chromosomes are known for 64 species of gerbils (Appendix 1). These data illustrate a range in diploid number (2N) from 18 in *Ammodillus imbellis* and females of *Taterillus petteri* to 74 in *Gerbillus dunni* and *G. latastei*. The distribution of diploid numbers in the species of gerbils that have been reported is plotted in Figure 1. In that

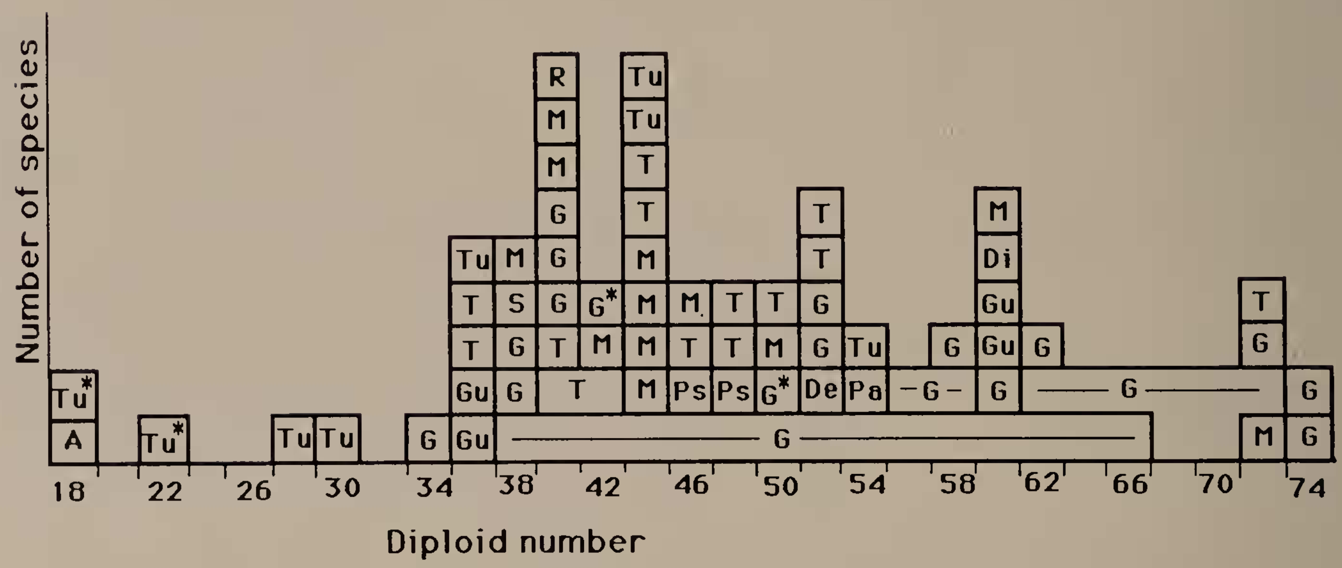

FIG. 1.—Distribution of diploid numbers in species of the family Gerbillidae. Intraspecific variability in diploid numbers is indicated by thin horizontal lines. Astericks indicate species with sex chromosome-autosome translocations (males have an odd diploid number). Abbreviations: A, *Ammodillus*; De, *Desmodillus*; Di, *Dipodillus*; G, *Gerbillus*; Gu, *Gerbillurus*; M, *Meriones*; Pa, *Pachyuromys*; Ps, *Psammomy*; S, *Sekeetamys*; T, *Tatera*; Tu, *Taterillus*.

figure, we show the number of species of each genus with particular diploid numbers. The genera *Tatera, Meriones,* and *Gerbillus* show extensive variability and include species with the highest recorded diploid numbers. These are also the genera with the greatest number of species (Lay, 1983; Carleton and Musser, 1984). Mean and median diploid numbers for gerbils coincide at 44. Species with a range in diploid number resulting from chromosome fusions or fissions, or both, do not affect these central values. This is observed by taking calculations using the highest and lowest diploid numbers possible. This mean or median diploid number of 44 is close to the proposed primitive karyotype (2N = 52) based on G-band analysis (Qumsiyeh, 1986*b*; Qumsiyeh and Chesser, 1988; and see below). From the evidence available it is quite likely that a species with a diploid number of 44 to 52 was the ancestor for all modern species of gerbillids. Higher and lower diploid numbers must have originated by chromosome fissions and fusions, which, on average, raised or lowered the diploid numbers of the effected taxa. However, fusions and fissions were not restricted to certain lineages as clearly some genera show both processes.

Unique insights into relationships and evolution in gerbils became possible with the advent of chromosomal banding techniques. Gamperl and Vistorin (1980) recorded homology of 11 chromosomal arms of *Meriones unguiculatus* with those of *Gerbillus campestris*, providing evidence for the feasibility of a phylogenetic study of gerbil chromosomes. In France, C- and R-banding techniques were used to assess homology among several species of gerbillids (Benazzou *et al.*, 1982*a*, 1982*b*, 1984). These papers documented some of the large amount of variation observed and suggested some basic homologies and relationships between certain groups. Other investigations in which differentially stained chromosomes have been utilized include the studies by Wassif (1981). That work was the first in which G- banded sex chromosomes in gerbils were examined and comments were made on the evolution of a sex chromosome complex (see below). The study was limited to eight species of the *Dipodillus-Gerbillus* complex including *Gerbillus calurus* (= *Sekeetamys calurus*). However, based on chromosomal, electrophoretic, and morphological data, the latter species is not a member of that group but is more closely related to species of the genus *Meriones* (Qumsiyeh and Chesser, 1988). Outgroups were not used in any of these earlier studies of chromosomal evolution in gerbils. When characters were used as synapomorphies (shared derived conditions), the most common condition was assumed to be primitive. However, this is not necessarily true and was shown to produce limited information in the case of the gerbillids (Qumsiyeh and Baker, 1988; Qumsiyeh, 1989). In our own studies of chromosomal evolution in this family, the outgroup method for determining primitive as opposed to derived character states was used and independent data sets (morphology and allozyme electrophoresis) were employed to test these relationships. The results of these studies can be summarized as follows.

1. It is possible to compare and find homologies for most or all euchromatic segments from all examined species of gerbils utilizing a standard numbering system for gerbil chromosomes (Qumsiyeh, 1986*b*, 1989; Qumsiyeh and Chesser, 1988; Qumsiyeh *et al.*, 1991).

2. Using this numbering system and including outgroup taxa (murids and sigmodontids), the primitive karyotype for the family Gerbillidae probably had a 2N = 52 and FN = 68 condition. This reconstructed karyotype was composed of acrocentric or telocentric autosomes 1, 2, 4d, 5, 6, 7, 8, 9, 10, 13, 14, 29, 30, 31, 32, and 33, and biarmed autosomes 3/4p, 11/12, 15/16, 17/18, 19/20, 21/22, 23/24, 25/26, and possibly 27/28 (Qumsiyeh, 1986*b*; Qumsiyeh and Chesser, 1988).

3. From this proposed primitive karyotype, chromosomal evolution in gerbils proceeded with centric fissions, centric fusions, paracentric and pericentric inversions, tandem fusions, translocations, and heterochromatic additions (Qumsiyeh, 1986*b*, 1989; Qumsiyeh and Chesser, 1988; Qumsiyeh *et al.*, 1991).

4. These chromosomal rearrangements provide reliable phylogenetic information on gerbils (as shown by concordance with results of studies

using electrophoresis and morphology) except in two situations. First, phylogenetic relationships of taxa with extensive Robertsonian rearrangements (centric fusions and fissions) can be obscured if one follows strict parsimony and no other data set is examined (Qumsiyeh et al., 1987; Qumsiyeh, 1989). Second, heterochromatin on some chromosomes provides no phylogenetic information in gerbils (Qumsiyeh, 1988).

Individual and geographic variation.—Geographic variation in number and morphology of chromosomes is common among rodents. Geographic variation in diploid numbers has been reported for several species of gerbils (for example, *Gerbillus campestris, G. pyramidum,* and *Tatera indica*). In well studied examples, variation in 2N is usually the result of Robertsonian translocations (for example, in *Gerbillus pyramidum* and *G. nigeriae*). Other types of geographic variation in gerbil chromosomes are additions and deletions of heterochromatin (Korobitsyna and Korablev, 1980; Qumsiyeh, 1986*b*; Qumsiyeh and Chesser, 1988) and euchromatin (Qumsiyeh, 1986*b*; Qumsiyeh *et al.*, 1987). An interesting variation recently discovered is the presence of interstitial C- banded regions in *Gerbillurus paeba* (Qumsiyeh *et al.*, 1991). Similar regions found in wild populations of *Mus musculus* were shown to represent homogeneously staining regions carrying amplified DNA (Traut *et al.*, 1984; Weith *et al.*, 1987).

Heterochromatin.—Patterns of heterochromatic distribution and variation in some species of gerbils have been reviewed by Qumsiyeh (1988). Heterochromatic additions in gerbils are extensive. In some taxa as much as one-third of the chromosomal material is C-band positive (Viegas-Péuignot *et al.*, 1984). As in other rodents, heterochromatic variations appear to provide little phylogenetic information. However, there are certain features of the heterochromatic distribution that are not easily explained. In many of the species of gerbils that have been studied, a pair of autosomes, corresponding to no. 33 of the standard numbering system for gerbils (Qumsiyeh, 1986*b*), appears to be completely heterochromatic. These species include members of diverse genera of gerbils (for example, *Meriones unguiculatus, Tatera leucogaster,* and *Gerbillurus paeba*). The function and significance of this observation remains to be elucidated.

Sex-determining mechanism.—Four of the 64 karyotypically characterized species of gerbils show autosome to sex chromosomes translocations, which result in a non-XX/XY sex-determining system (Appendix). These four species are *Gerbillus gerbillus, G. gleadowi, Taterillus gracilis,* and *T. petteri*. Detailed studies implicated both

X- and Y-autosome translocations in these species (Wassif, 1977, 1981; Wahrman *et al.*, 1983; Viegas-Péquignot *et al.*, 1984).

Meiotic studies.—Synaptonemal complex analyses in gerbils have contributed to understanding the behavior and origin of sex chromosomes (Wahrman *et al.*, 1983). Our understanding of the behavior of synaptonemal complexes in general has also been advanced by studies on gerbils. The classical studies on XY synapsis (Solari and Ashley, 1977) and the synapsis in inversion loops (Ashley and Moses, 1980; Ashley *et al.*, 1981) in *Psammomys obesus* provided the impetus for further development of this field of cytogenetic investigation.

Conclusions

The extensive karyotypic diversity in the family Gerbillidae contrasts sharply with the limited morphological evolution found in the family and provides an example of accelerated karyotypic evolution. Chromosomal rearrangements reported in gerbils include centric fusions, centric fissions, tandem fusions, pericentric and paracentric inversions, translocations, euchromatic additions and deletions, and heterochromatic additions and deletions. Intraspecific geographic variation in chromosomal rearrangements also appears to be common in gerbils.

Studies of the rich chromosomal evolution in gerbils combined with recent new studies of variation in morphology and proteins should continue to provide empirical data needed to test the many hypotheses concerning chromosomal evolution and speciation. The feasibility of collecting samples and establishing laboratory colonies in gerbils adds to the benefits of using them as models for studying chromosomal evolution in mammals.

Literature Cited

Al-Saleh, A. A., and M. A. Khan. 1987. Cytological studies of certain desert mammals of Saudi Arabia. 5. The karyotype of *Meriones rex*. Genetica, 73:185–187.

Ashley, T., and M. J. Moses. 1980. End association and segregation of the achiasmatic X and Y chromosomes of the sand rat, *Psammomys obesus*. Chromosoma, 78:203–210.

Ashley, T., M. J. Moses, and A. J. Solari. 1981. Fine structure and behavior of a pericentric inversion in the sand rat *Psammomys obesus*. J. Cell Sci., 50:105–119.

Benazzou, T., and H. Genest-Villard. 1980. Une nouvelle espèce de gerbille au Maroc: *Gerbillus hesperinus* Cabrera, 1906 (rongeurs, gerbillidés). Mammalia, 44:410–412.

Benazzou, T., E. Viegas-Pequignot, F. Petter, and B. Dutrillaux. 1982*a*. Phylogénie chromosomique de quatre espèces de *Meriones* (rongeur, Gerbillidae). Ann. Génét., 25:19–24.

———. 1982*b*. Phylogénie chromosomique des Gerbillidae. Etude de six *Meriones*, de *Taterillus gracilis* et de *Gerbillus tytonis*. Ann. Génét., 25:212–217.

Benazzou, T., E. Viegas-Pequignot, M. ProdHomme, M. Lombard, F. Petter, and B. Dutrillaux. 1984. Phylogénie chromosomique des Gerbillidae. III. Etude d'espèces des genres *Tatera, Taterillus, Psammomys* et *Pachyuromys*. Ann. Génét., 27:17–26.

Capanna, E., and M. S. Merani. 1981. Karyotypes of Somalian rodent populations. 2. The chromosomes of *Gerbillus dunni* (Thomas, 1904), *Gerbillus pusillus* Peters, 1878 and *Ammodillus imbelis* (De Winton, 1898). Monit. Zool. Ital., Suppl. 14:199–226.

Carleton, M. D., and G. G. Musser. 1984. Muroid rodents. Pp. 289–379, *in* Orders and families of Recent mammals of the world (S. Anderson and J. K. Jones, eds), John Wiley & Sons, Inc., New York, xii+686 pp.

Chaline, J., P. Mein, and F. Petter. 1977. Les grandes lignes d'une classification évolutive des Muroidea. Mammalia, 41:245–252

Cockrum, E. L., P. J. Vaughan, and T. C. Vaughan. 1977. Status of the pale sand rat, *Psammomys vexillaris* Thomas, 1925. Mammalia, 41:321–326.

Cockrum, E. L., T. C. Vaughan, and P. J. Vaughan. 1976*a*. A review of North African short-tailed gerbils (*Dipodillus*) with description of a new taxon from Tunisia. Mammalia, 40:313–326.

———. 1976*b*. *Gerbillus andersoni* de Winton, a species new to Tunisia. Mammalia, 40:467–473.

Gamperl, R., and G. Vistorin. 1978. Studies on Gerbillinae (Rodentia) I. Banding patterns of mitotic and meiotic chromosomes of the Mongolian gerbil, *Meriones unguiculatus*. Z. Säugetierk., 43:278–282.

———. 1980. Comparative study of G- and C-banded chromosomes of *Gerbillus campestris* and *Meriones unguiculatus* (Rodentia, Gerbillinae). Genetica, 52/53:93–97.

Gautun, J. C., M. Tranier, and B. Sicard. 1985. Liste préliminaire des rongeurs du Burkina Faso (ex Haute-Volta). Mammalia, 49:537–542.

Genest, H., and F. Petter. 1973. Les *Taterillus* de Republique Centrafricaine (rongeurs, gerbillidés). Mammalia, 37:66–75.

Gordon, D. H., and I. L. Ratenbach. 1980. Species complexes in medically important rodents: chromosome studies of *Aethomys, Tatera,* and *Saccostomus* (Rodentia: Muridae, Cricetidae). South African J. Sci., 76:559561.

Heptner, W. G. 1933. Notizen über die Gerbillidae (Mammalia, Rodentia). VI. Über die einteilung der Gerbillidae. Zool. Anz., 102:107–112.

Hsu, T. C., and K. Benirschke. 1967–1971. An atlas of mammalian chromosomes. Springer Verlag, New York (loose leaf).

Hubert, B. 1978. Caryotype de *Gerbillus pulvinatus* Rhoads, 1896 (rongeurs, gerbillidés) de la vallee l'Omo (Ethiopie). Mammalia, 42:225–228.

Hubert, B., F. Adam, and A. Poulet. 1973. Liste préliminaire des rongeurs du Senegal. Mammalia, 37:76–87.

Hubert, B., and W. Bohme. 1978. Karyotype of *Gerbillus pyramidum* I. Geoffroy (Rodentia, Gerbillidae) from Senegal. Bull. Carnegie Mus. Nat. Hist., 6:38–40.

Jordan, R. G., B. L. Davis, and H. Baccar. 1974. Karyotypic and morphometric studies of Tunisian *Gerbillus*. Mammalia, 38:667–680.

Jotterand-Bellomo, M. 1984. New developments in vertebrate cytotaxonomy. VII Les Chromosomes des rongeurs (order Rodentia Bowdich, 1821). Genetica, 64:3–64.

Korobitsyna, K. V. 1969. [Intraspecific variability of chromosomes of some species of gerbils (Meriones, Gerbillinae, Cricetidae, Rodentia)]. Pp. 117–120, *in* The mammals (evolution, taxonomy, fauna) (N. N. Vorontsov, ed.), Acad. Sci. USSR, Novosibirsk (in Russian), 167 pp.

Korobitsyna, K. V., and V. P. Korablev. 1980. The interspecific autosome polymorphism of *Meriones tristrami* Thomas, 1892 (Gerbillinae, Cricetidae, Rodentia). Genetica, 52/53:209–221.

Lay, D. M. 1975. Notes on rodents of the genus *Gerbillus* (Mammalia: Muridae: Gerbillinae) from Morocco. Fieldiana Zool., 65:89–101.

———. 1983. Taxonomy of the genus *Gerbillus* (Rodentia: Gerbillinae) with comments on the applications of generic and subgeneric names and an annotated list of species. Z. Säugetierk., 48:329–354.

Lay, D. M., and C. F. Nadler. 1975. A study of of *Gerbillus* (Rodentia: Muridae) east of the Euphrates river. Mammalia, 39:423–445.

Lay, D. M., K. Agerson, and C. F. Nadler. 1975. Chromosomes of some species of *Gerbillus* (Mammalia, Rodentia). Z. Säugetierk., 40:141–150.

Matthey, R. 1952. Chromosomes sexuals multiples chez un rongeur (Gerbillus pyramidum Geoffroy). Archiv Klaus-Stiftung Vererbungsforsch. 27:163–167.

———. 1953. Les chromosomes des Muridae: révision critique et matériaux nouveaux pour service à l'histoire de l'évolution chromosomique ches les rongeurs. Rev. Suisse Zool., 60:225–283.

———. 1954*a*. Nouvelles donnees sur les formules chromosomiques des Muridae. Experientia, 10:66–67.

———. 1954*b*. Nouvelles recherches sur les chromosomes des Muridae. Caryologia, 6:1–44.

———. 1957. Cytologie et taxonomie du genre *Meriones* Illiger (Rodentia: Muridae: Gerbillinae). Säugetierk. Mitt., 5:145–150.

———. 1958. Les chromosomes et la position systématique de quelque Murinae Africains (Mammalia-Rodentia). Acta Tropica, 15:97–117.

———. 1969. Chromosomes de Gerbillinae. Genres *Tatera* et *Taterillus*. Mammalia, 33:522–528.

Matthey, R., and M. Jotterand. 1972. L'analyse du caryotype parment de reconnaitre deux espèces cryptiques confondues sous de le *Taterillus gracilis* (TH) (rongeurs, Gerbillidae). Mammalia, 36:183–209.

Matthey, R., and F. Petter. 1970. Etude cytogénétique et taxonomique de 40 *Tatera* et *Taterillus* provenant de Haute-Volta et Republique Centrafricaine (rongeurs, Gerbillidae). Mammalia, 34:585–597.

Nadler, C. F., and D. M. Lay. 1968. Chromosomes of some species of Meriones (Mammalia: Rodentia). Z. Säugetierk., 32:285–291.

Nadler, C. F., D. M. Lay, and J. D. Hassinger. 1969. Chromosomes of three Asian mammals: *Meriones meridianus* (Rodentia: Gerbillinae), *Spermophilopsis leptodactylus* (Rodentia: Sciuridae), *Ochotona rufescens* (Lagomorpha: Ochotonidae). Experientia, 25:774–775.

Nowak, R. M., and J. L. Paradiso. 1983. Walker's Mammals of the World. Johns Hopkins Univ. Press, Baltimore, Maryland, 2:viii+569–1362+xi-xxv.

Orlov, V. N. 1969. [The chromosome complement of some species of Meriones from Armenia)]. Pp. 121–123, *in* The mammals (evolution, taxonomy, fauna) (N. N. Vorontsov, ed.), Acad. Sci. USSR, Novosibirsk (in Russian), 167 pp.

Orlov, V. N., S. I. Radjabli, V. M. Malygin, N. Chotolchu, J. M. Kovalskaja, N. S. Bulatova, and M. I. Baskevic. 1978. [Karyotypes of the mammals of Mongolia].

Geografija i dinamika rastitelnigo i zivotnogo mira MNR Nauka, Moskva, 149–164 (in Russian).

Pavlinov, I. Y. 1982. [Phylogeny and classification of the subfamily Gerbillinae]. Byull. Mosk. Obshch. Ispyt. Prirody, Otd. Biol., 87:19–31. (in Russian, English translation no. 1598, Med. Zool. Dept., U.S. NAMRU-3, Cairo, Egypt).

Qumsiyeh, M. B. 1986*a*. Chromosomal evolution in the rodent family Gerbillidae. Ph.D. dissertation, Texas Tech Univ., Lubbock, 109 pp.

———. 1986*b*. Phylogenetic studies of the rodent family Gerbillidae: I. Chromosomal evolution in the Southern African complex. J. Mamm., 67:680–692.

———. 1988. Pattern of heterochromatic variation and phylogeny in the rodent family Gerbillidae. Texas J. Sci., 40:63–70.

———. 1989. Chromosomal fissions and phylogenetic hypotheses: Cytogenetic and allozymic variation between species of Meriones (Rodentia, Gerbillidae). Occas. Papers Mus., Texas Tech Univ., 132:1–16.

Qumsiyeh, M. B., and R. J. Baker. 1988. Comparative cytogenetics and the determination of primitive karyotypes. Cytogenet. Cell Genet., 47:100–103.

Qumsiyeh, M. B., and R. K. Chesser. 1988. Rates of protein, chromosome, and morphologic evolution in four genera of Rhombomyine gerbils. Biochem. Syst. Ecol., 16:89–103.

Qumsiyeh, M. B., M. J. Hamilton, and D. A. Schlitter. 1987. Problems of using Robertsonian rearrangements in determining monophyly: examples from the genera *Tatera* and *Gerbillurus*. Cytogenet. Cell Genet., 44:198–208.

Qumsiyeh, M. B., D. A. Schlitter, and A. M. Disi. 1986. New records and karyotypes of small mammals from Jordan. Z. Säugetierk., 51:139–146.

Qumsiyeh, M. B., M. J. Hamilton, E. R. Dempster, and R. J. Baker. 1991. Cytogenetics and systematics of the rodent genus *Gerbillurus*. J. Mamm., 72:89–96.

Ratomponirina, C., E. Viegas-Pequignot, B. Dutrillaux, F. Petter, and Y. Rumpler. 1986. Synaptonemal complexes in the Gerbillidae: probable role of intercalated heterochromatin in *gonosome*-autosome translocations. Cytogenet. Cell Genet., 43:161–167.

Robbins, C. B. 1973. Systematic status and karyotypic relationships of the genus *Taterillus* (Rodentia: Cricetidae) from Kenya. Mammalia, 37:642–645.

———. 1974. Comments on the taxonomy of the west African *Taterillus* (Rodentia: Cricetidae) with the description of a new species. Proc. Biol. Soc. Washington, 87:395–404.

Schlitter, D. A., I. L. Rautenbach, and C. G. Coetzee. 1984. Karyotypes of southern African gerbils, genus *Gerbillurus* Shortridge, 1942 (Rodentia, Cricetidae). Ann. Carnegie Mus. Nat. Hist., 53:549–557.

Sicard, B., M. Tranier, and J.-C. Gautun. 1988. Un rongeur nouveau du Burkina Faso (ex Haute-Volta): *Taterillus pettersi*, sp. nov. (Rodentia, Gerbillidae). Mammalia, 52:187–198.

Smith, A. G., D. B. Hackel, and K. Schmidt-Nielson. 1966. Chromosomes of the sand rat (*Psammomys obesus*). Canadian J. Genet. Cytol., 8:756–758.

Solari, A. J., and T. Ashley. 1977. Ultrastructure and behavior of the achiasmatic, telosynaptic XY pair of the sand rat (*Psammomys obesus*). Chromosoma, 62:319–336.

Tranier, M. 1974*a*. Dimorphisme chromosomique dans une population de *Tatera* du sud du Tchad (rongeurs, Gerbillidae). Mammalia, 38:224–233.

———. 1974*b*. Polymorphism chromosomique multiple chez des *Taterillus* du Niger (rongeurs, gerbillides). Compte Rendue du Acad. Sci. Paris, ser. D, 278: 3347–3350.

———. 1975. Originalité du caryotype de *Gerbillus nigeriae* (rongeurs, gerbillidés). Mammalia, 39:703–704.

Tranier, M., B. Hubert, and F. Petter. 1974. *Taterillus* de l'ouest du Tchad et du nord du Cameroun (rongeurs, gerbillidés). Mammalia, 37:637–641.

Traut, W., H. Winking, and S. Adolph. 1984. An extra segment in chromosome 1 of wild *Mus musculus*: a C-band positive homogenously staining region. Cytogenet. Cell Genet., 38:290–297.

Viegas-Péquignot, E., T. Benazzou, B. Dutrillaux, and F. Petter. 1982. Complex evolution of sex chromosomes in Gerbillidae (Rodentia). Cytogenet. Cell Genet., 34:158–167.

Viegas-Péquignot, E., T. Benazzou, M. ProdHomme, and B. Dutrillaux. 1984. Characterisation of a very complex constitutive heterochromatin in two *Gerbillus* species (Rodentia). Chromosoma, 89:42–47.

Viegas-Péquignot, E., D. Petit, T. Benazzou, M. Prod'Homme, M. Lombard, F. Hoffschir, J. Descailleux, and B. Dutrillaux. 1986. Phylogénie chromosomique chez les Sciuridae, Gerbillidae et Muridae, et étude d'espèces appartenant a d'autres familles de rongeurs. Mammalia, 50:175–202.

Vistorin, G., and R. Gamperl. 1978. Studies on Gerbillinae (Rodentia). 2. The karyotype of *Gerbillus campestris*, analysed by G- and C-banding techniques. Z. Säugetierk., 43:369–373.

Volobouev, V. T., E. Viegas-Péquignot, F. Petter, J.-C. Gautin, B. Sicard, and B. Dutrillaux. 1988. Complex chromosomal polymorphism in *Gerbillus nigeria* (Rodentia, Gerbillidae). J. Mamm., 69:131–134.

Vorontsov, N. N., and K. V. Korobitsyna. 1969. [The comparative karyology of the highest gerbils (genera Meriones and Rhombomys: Gerbillinae, Rodentia)] (In Russian). Pp. 111–116, *in* The mammals (evolution, taxonomy, fauna) (N. N. Vorontsov, ed.), Acad. Sci. USSR, Novosibirsk, 167 pp.

———. 1970. [Materials on comparative karyology of Gerbillinae]. Citologija, 12:152–157. (in Russian with English summary).

Wahrman, J., C. Richler, E. Neufeld, and A. Friedman. 1983. The origin of multiple sex chromosomes in the gerbil *Gerbillus gerbillus* (Rodentia: Gerbillidae). Cytogenet. Cell Genet., 35:161–180.

Wahrman, J., C. Richler, and U. Ritze. 1988. Chromosomal considerations in the evolution of the Gerbillinae of Israel and Sinai. Pp. 439–485, *in* The zoogeography of Israel (Y. Yom-Tov and E. Tchernov, eds.), Dr. W. Junk Publishers, Dordrecht, Netherlands, viii+600 pp.

Wahrman, J., and A. Zahavi. 1955. Cytological contributions to the phylogeny and classification of the rodent genus *Gerbillus*. Nature, 175:600–602.

Wassif, S. 1977. Untersuchungen uber Verwandtschaft bezeihungen in den genera *Gerbillus* und *Dipodillus* unter anwendung der Chromosomen-Bandentechniken. Doctoral dissertation, Georg-August-Universitat, Göttingen, 149 pp.

———. 1981. Investigations on the relationships of the genera *Gerbillus* and *Dipodillus* (Rodentia, Cricetidae) by the use of chromosome banding techniques. Bull. Zool. Soc. Egypt, 31:139–155.

Wassif, K., R. G. Lutfy, and S. Wassif. 1969. Morphological, cytological and taxonomic studies of the rodent genera *Gerbillus* and *Dipodillus* from Egypt. Proc. Egyptian Acad. Sci., 22:77–96.

Weith, A., H. Winking, B. Brackmann, B. Boldyreff, and W. Traut. 1987. Microclones from a mouse germ line HSR detect amplification and complex rearrangements of DNA sequences. The EMBO J., 6:1295–1300.

Yosida, T. H. 1981. Chromosome polymorphism of the large naked-soled gerbil, *Tatera indica* (Rodentia, Muridae). Japanese J. Genet., 56:241–248.

Zahavi, A., and J. Wahrman. 1957. The cytotaxonomy, ecology and evolution of the gerbils and jirds of Israel (Rodentia: Gerbillinae). Mammalia, 21:341–380.

Addresses of authors: *Division of Genetics, Room 523, The University of Tennessee Medical School, 711 Jefferson Ave., Memphis, Tennessee 38163* (MBQ) and *Section of Mammals, The Carnegie Museum of Natural History Annex, 5800 Baum Boulevard, Pittsburgh, Pennsylvania 15206–3706* (MBQ, DAS). Present address of MBQ: *Cytogenetics Lab, T.C. Thompson Children's Hospital Medical Center, 910 Blackford Street, Chattanooga, Tennessee 37403.* *Received 11 March 1991; accepted 8 April 1991.*

APPENDIX—*Karyotypic data for gerbils.*

The diploid number is given for each species followed by the number of metacentric and submetacentric autosomes (B), the numbers of acrocentric and telocentric autosomes (A), the size (small letters) and shape (capital letters) of the X and Y chromosomes, general locality or country of origin of samples, and recent references. Some authors include sex chromosomal arms in counts of fundamental numbers, others only autosomal arms. Because of this, we give the number of biarmed autosomes (B) and numbers of acrocentric autosomes (A) rather than the fundamental number (unless this information is not obtainable from these references). In cases where the authors did not separate the sex chromosomes, we indicate this condition with an asterick under column "B."

Species	2N	B	A	X	Y	Locality	Banding	Reference
Ammodillus imbelis	18	18*	0	–	–	Somalia	–	(Capanna and Merani, 1981)
Brachiones przewalski	No data							
Desmodilliscus baueri	No data							
Desmodillus auricularis	52	–	–	–	–	S. Africa	–	(Matthey, 1954*b*)
	52	28	22	lM	mM	S. Africa	G,C	(Qumsiyeh, 1986*b*)
Dipodillus maghrebi	No data							
Dipodillus simoni	60	8-10	48-50	–	–	Egypt	–	(Wassif *et al.*, *1*969)
	60	0	58	lM	sSM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	60	8-10	48-50	–	–	Tunisia	–	(Cockrum *et al.*, 1976*a*)
Gerbillurus paeba	36	–	–	–	–	S. Africa	–	(Matthey, 1958)
	36	34	0	mSM	sA	S. Africa, Namibia	–	(Schlitter *et al.*, 1984)
	36	34	0	mSM	sA/sB	S Africa, Namibia	G,C	(Qumsiyeh, 1986*b*; Qumsiyeh *et al.*, 1991)
Gerbillurus setzeri	60	18	40	lSM	sA	Namibia	–	(Schlitter *et al.*, 1984)
	60	20	38	lSM	sA	Namibia	G,C	(Qumsiyeh *et al.*, 1991)
Gerbillurus tytonis	36	34	0	SM	–	Namibia	R	(Benazzou *et al.*, 1982*b*)
	36	34	0	mSM	sA	Namibia	–	(Schlitter *et al.*, 1984)
	36	34	0	lSM	sA	Namibia	G,C	(Qumsiyeh *et al.*, 1991)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Gerbillurus vallinus	60	22	36	1M	sA	S. Africa, Namibia	—	(Schlitter *et al.*, 1984
	60	12-20	38-46	1SM	sA	S. Africa, Namibia	G,C	(Qumsiyeh, 1986*b*; Qumsiyeh *et al.*, 1991)
Gerbillus agag	No data							
Gerbillus andersoni (= *allenbyi*)	40	38	0	1SM	sSM	Egypt	–	(Wassif *et al.*, 1969)
	40	38	0	1SM	mSM	Egypt	–	(Lay, 1975)
	40	38	0	lSM	SM	Israel	–	(Wahrman *et al.*, 1988)
	40	38	0	1SM	sSM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	40	38	0	–	–	Tunisia	–	(Cockrum *et al.*, 1976*b*)
	40	38	0	–	–	Israel	–	(Wahrman and Zahavi, 1955)
Gerbillus aquilus	38	36	0	1SM	sM	Pakistan, Iran	–	(Lay, 1975) (Lay and Nadler, 1975)
Gerbillus bottai	No data							
Gerbillus campestris	56	–	–	SM	SM	Algeria	–	(Matthey, 1953)
	56	13-15	41-43	–	–	Egypt	–	(Wassif *et al.*, 1969)
	58	8	48	1M	mM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	56, 57, 58	10-12	44-48	mM	sA	Morocco	–	(Lay, 1975)
	56	14	40	1Ms	SM	Morocco	G,C	(Vistorin and Gamperl, 1978; Gamperl and Vistorin, 1980)
	56	14	40	1SM	sSM	Tunisia	–	(Jordan *et al.*, 1974)
Gerbillus cheesmani	38	34	2	mM	sM	Iran	–	(Lay, 1975; Lay and Nadler, 1975)
	38	34	2	mSM	sM	Iran	–	(Hsu and Benirschke, 1967–1971)
	38	–	–	SM	SM	Saudi Arabia	C	(Ratomponirina *et al.*, 1986)
	38	36	–	M	–	–	R	(Viegas-Péquignot *et al.*, 1986)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Gerbillus dasyurus	60	6-8*	52-54	–	–	Sinai	–	(Wahrman and Zahavi, 1955)
	60	6	52	lM	–	Sinai	–	(Lay *et al.*, 1975; Lay and Nadler, 1975)
	60	9-10	50-51	–	–	Egypt	–	(Wassif *et al.*, 1969)
	60	8-12	46-50	lM	sA	Jordan, Palestine	G,C	(Qumsiyeh, 1986*b*)
Gerbillus dunni	74	24	48	lSM	mM	Somalia	–	(Capanna and Merani, 1981)
Gerbillus famulus	No data							
Gerbillus gerbillus	42,43	–	–	–	Y1, Y2	Algeria	–	(Matthey, 1953; Matthey, 1954*a*)
	42,43	38-40*	–	lSM	Y1,Y2	Israel	–	(Wahrman and Zahavi, 1955)
	42	32	8	lSM	–	Morocco	–	(Lay *et al.*, 1975)
	42,43	32	8	lSM	Y1=sM	Egypt	–	(Lay *et al.*, 1975; Lay and Nadler, 1975)
	42,43	34	6	lSM	Y1=SM Y2=SM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	42,43	34-36	–	lSM	Y1=A Y2=A	Egypt	–	(Wassif *et al.*, 1969)
	42,43	36	6	lSM	–	Tunisia	–	(Jordan *et al.*, 1974)
	42,43	32	8	lA	Y1=sSM Y2=sSM	Egypt	–	(Hsu and Benirschke, 1967-1971)
	42,43	36	6	SM	M,M	Israel	G,C	(Wahrman *et al.*, 1983)
Gerbillus gleadowi	50,51	20	28	lSM	mA,mM	Pakistan	–	(Hsu and Benirschke, 1967–1971; Lay *et al.*, 1975; Lay and Nadler, 1975)
Gerbillus henleyi	52	11-13	39-48	–	–	Egypt	–	(Wassif *et al.*, 1969)
	52	8	42	lSM	sA	Morocco	–	(Lay *et al.*, 1975)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Gerbillus hesperinus	58	22	34	lSM	M	Morocco	–	(Lay *et al.*, 1975)
	58	20	36	lM	mM	Morocco	–	(Lay, 1975)
	58	22	34	lSM	M	Morocco	–	(Benazzou and Genest-Villard, 1980)
	58	22	34	lSM	M	Morocco	R,C,Q	(Viegas-Péquignot *et al.*, 1984)
Gerbillus hoogstraali	72	6	64	lSM	mM	Morocco	–	(Lay, 1975)
	72	6	64	lSM	lM	Morocco	–	(Lay *et al.*, 1975)
	72	–	–	lSM	M	Morocco	R	(Ratomponirina *et al.*, 1986; Viegas-Péquignot *et al.*, 1986)
Gerbillus jamesi	No data							
Gerbillus latastei (as *G. aureus*)	74	20-28	44-52	lSM	A	Tunisia	–	(Jordan *et al.* , 1974; Cockrum *et al.*, 1976)
Gerbillus mackillingi	No data							
Gerbillus mauritaniae	No data							
Gerbillus mesopotamiae	No data							
Gerbillus muriculus	No data							
Gerbillus nancilus	No data							
Gerbillus nanus	54	–	–	lSM	lSM	Algeria	–	(Matthey, 1954*a*)
	52	10-14*	36-40	–	–	Israel	–	(Wahrman and Zahavi, 1955)
	52	8	42	lM	sA	Morocco	–	(Lay *et al.*, 1975; Lay and Nadler, 1975)
	52	8	42	lM	sA	Tunisia	–	(Jordan *et al.*, 1974)
	52	9-10*	42-43	–	–	Egypt	–	(Wassif *et al.*, 1969)
	52	8	44	lSM	sA	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	52	10	40	lSM	sA	Jordan	G,C	(Qumsiyeh *et al.*, 1986)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Gerbillus nigeriae	68-72	(variable)		lSM	mM	Burkina Faso	–	(Volobouev *et al*., 1988)
	62-68	>30	–	lA	–	Niger	–	(Tranier, 1975)
	72	–	–	lA	M	Niger	R,C,Q	(Viegas-Péquignot *et al*., 1984)
	72	–	–	A	M	Burkina Faso	R	(Ratomponirina *et al*., 1986)
	67-68	–	–	–	–	Burkina Faso	–	(Gautun *et al*., 1985)
Gerbillus occiduus	40	38	0	mM	mM	Morocco	–	(Lay, 1975)
Gerbillus perpallidus	40	34	4	lSM	sM	Egypt	–	(Lay *et al*., 1975)
	40	34	4	lSM	sM	Egypt	G	(Wassif, 1977, 1981)
Gerbillus poecilops	No data							
Gerbillus pulvinatus	62	20	40	M?	M?	Ethiopia	–	(Hubert, 1978)
Gerbillus pusillus	34	18	14	mA	sM	Somalia	–	(Capanna and Merani, 1981)
Gerbillus pyramidum	40	36	2	–	–	Algeria	–	(Matthey, 1952; Matthey, 1953)
	38	36	0	lSM	sM	Egypt	–	(Wassif *et al*., 1969; Lay *et al*., 1975; Wassif, 1977, 1981)
	40	36	2	lM	lM	Tunisia	–	(Jordan *et al*., 1974)
	40	–	–	–	–	Senegal	–	(Hubert and Bohme, 1978)
	40-66 variable		–	–	–	Sinai, Israel	–	(Wahrman and Zahavi, 1955; Zahavi and Wahrman, 1957)
	50-52	26-24	24-28	SM	M	Israel/Coast	C,B	(Wahrman *et al*., 1983)
	64-66	12-10	52-56	SM	M	Negev/Sinai	C,B	(Wahrman *et al*., 1983)
Gerbillus riggenbachi	No data							
Gerbillus rosalinda	No data							
Gerbillus ruberrimus	No data							
Gerbillus syrticus	No data							
Gerbillus watersi	No data							
Meriones changi	No data							

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Meriones crassus	60	–	–	–	–	Israel	–	(Zahavi and Wahrman, 1957)
	60	10	48	lSM	mSM	Egypt, Iran	–	(Nadler and Lay, 1968)
	60	12	46	lSM	–	Iran	R	(Benazzou *et al.*, 1982*b*)
	60	12	48	lSM	mM	Jordan	G,C	(Qumsiyeh *et al.*, 1986)
Meriones hurrianae	40	36	2	lSM	SM	Iran	–	(Nadler and Lay, 1968)
Meriones libycus	44	–	–	–	–	–	–	(Matthey, 1953)
(incl. *erythrourus*)	44	30	12	lA	sSM	USSR	–	(Vorontsov and Korobitsyna, 1969)
	44	30	12	lA	mSM	Iran	–	(Nadler and Lay, 1968)
	44	30	12	lA	mSM	Iran	R	(Benazzou *et al.*, 1982*b*)
	44	30	12	–	–	Jordan	G	(Qumsiyeh, 1986*b* as *shawi*)
Meriones meridianus	50	26	22	lM	sA variable	USSR	–	(Korobitsyna, 1969; Orlov, 1969; Vorontsov and Korobitsyna, 1969, 1970)
	50	26	22	lM	sSM	Mongolia	–	(Nadler *et al.*, 1969; Orlov *et al.*, 1978)
Meriones persicus	42	34	6	lSM	mSM	Iran	–	(Matthey, 1957)
	42	34	6	lSM	–	Iran	R	(Benazzou *et al.*, 1982*b*)
	42	34	6	lSM	mSM	USSR	–	(Vorontsov and Korobitsyna, 1969, 1970)
Meriones rex	38	34	2	mM	sM	Saudi Arabia	–	(Al-Saleh and Khan, 1987)
Meriones sacramenti	46	–	–	–	–	Israel	–	(Zahavi and Wahrman, 1957)
Meriones shawi	44	32	10	–	–	–	–	(Matthey, 1957)
	44	30	12	lSM	mSM	Egypt	–	(Hsu and Benirschke, 1967–1971)
	44	30	12	lSM	mSM	Morocco	R	(Benazzou *et al.*, 1982*b*)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Meriones tamariscinus	40	36	2	lM	–	USSR	–	(Vorontsov and Korobitsyna, 1969, 1970)
	40	36	2	lM	sSM	USSR	–	(Orlov *et al.*, 1978)
Meriones tristrami	72	0	70	–	–	–		(Matthey, 1957)
	72	0	70	lSM	–	Iran	R	(Benazzou *et al.*, 1982*a*, 1982*b*)
	72	6-19	51-64	lSM	sSM	USSR	C	(Olov, 1969; Vorontsov and Korobitsyna, 1969; Korobitsyna and Korablev, 1980)
	72	4	66	–	–	Israel	–	(Zahavi and Wahrman, 1957)
	72	0-6	64-70	–	–	Jordan	R	(Qumsiyeh, 1986*b*, 1988)
Meriones unguiculatus	44	32	10	lSM	mSM	Domestic	–	(Nadler and Lay, 1968)
	44	32	10	lSM	mSM	Domestic	G,C	(Gamperl and Vistorin, 1978; Qumsiyeh and Chesser, 1988)
	44	32	10	lSM	sSM	Mongolia	–	(Korobitsyna, 1969; Vorontsoy and Korobitsyna, 1969)
	44	32	10	lSM	sSM	Domestic	G	(Gamperl and Vistorin, 1980)
Meriones vinogradovi	44	32	10	–	–	–	–	(Matthey, 1954*b*)
	44	32	10	–	–	Iran	–	(Nadler and Lay, 1968)
	44	32	10	lM	sM	USSR	–	(Orlov, 1969; Vorontsov and Korobitsyna, 1969, 1970; Orlov *et al.*, 1978)
Meriones zarudnyi	No data							
Microdillus peeli	No data							
Pachyuromys duprasi	54	10	42	SM	–	Morocco	R	(Benazzou *et al.*, 1984)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Psammomys obesus	48	24	22	lM	sM	Captive	–	(Smith *et al.*, 1966)
	48	28	18	lSM	sSM	Captive	–	(Hsu and Benirschke, 1967–1971)
	48	28	18	lM	mM	Captive	C	(Solari and Ashley, 1977)
	48	28	18	lM	mM	Jordan	G,C	(Qumsiyeh, 1986*b*, 1988)
	48	28	18	lM	M	Tunisia	–	(Cockrum *et al.*, 1977)
Psammomys vexillaris	46	30	14	lM	–	Tunisia	–	(Cockrum *et al.*, 1977)
Rhombomys opimus	40	36	2	lSM	sM	Mongolia	–	(Vorontsov and Korobitsyna, 1969)
Sekeetamys calurus	38	32-36*	–	–	–	Sinai	–	(Wahrman and Zahavi, 1955)
	38	34	2	lM	sA	Egypt	–	(Wassif *et al.*, 1969; Wassif, 1977, 1981)
	38	34	2	lSM	–	Sinai	G	(Qumsiyeh and Chesser, 1988)
Tatera afra	44	NF=70-76		–	–	S. Africa	–	(Matthey, 1954*b*)
	44	24	30	lSM	mM	S. Africa	G	(Qumsiyeh, 1986*b*)
Tatera boehmi	No data							
Tatera brantsii	44	NF=70-76		M	M	S. Africa	–	(Matthey, 1954*b*)
	44	24	20	lSM	mM	S. Africa	G,C	(Qumsiyeh, 1986*b*)
Tatera gambiana	52	–	–	–	–	Senegal	–	(Hubert *et al.*, 1973)
Tatera guineae	50	16	32	lSM	A	Burkina Faso	–	(Matthey and Petter, 1970)
	50	16	32	lSM	A	Burkina Faso	R	(Benazzou *et al.*, 1984; Gautun *et al.*, 1985)
Tatera hopkinsoni	48	16	30	lA	A	Burkina Faso	–	(Matthey and Petter, 1970; Gautun *et al.*, 1985)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Tatera inclusa	No data							
Tatera indica	72	NF=80	–	–	–	–	–	(Matthey, 1953)
	68	16	50	lM	sA	India	–	(Yosida, 1981)
Tatera kempi	36	28	6	lSM	mSM	C. African Republic	–	(Matthey and Petter, 1970—prob. *T. robusta*, Qumsiyeh *et al*., 1987)
Tatera leucogastor	42	NF=72	–	M	–	S. Africa	–	(Matthey, 1954*b*; Matthey, 1958)
	40	28	10	mSM	lSM	S. Africa	–	(Gordon and Ratenbach, 1980)
	40	28	10	lSM	sSM	S. Africa, Namibia	–	(Qumsiyeh, 1986*b*)
Tatera nigricauda	40	32	6	lSM	mSM	Ethiopia	–	(Matthey, 1969)
	40	32	6	lSM	–	Kenya	G,C	(Qumsiyeh *et al*., 1987)
Tatera nigrita	48	16	30	lSM	A	Burkina Faso	–	(Matthey and Petter, 1970)
	48	16	30	lSM	A	C. African Republic, Chad	–	(Tranier, 1974*a*—X polymorphic)
	48	16	30	lSM	A	C. African Republic	R	(Benazzou *et al*., 1984)
Tatera phillipsi	46	20	24	lSM	mSM	C. African Republic	–	(Matthey and Petter, 1970; Qumsiyeh *et al*., 1987)
Tatera robusta	36	34	0	lSM	sSM	Kenya	G,C	(Qumsiyeh *et al*., 1987)
Tetera valida	52	14	36	lSM	–	Senegal	–	(Matthey, 1969)
Taterillus angelus	No data							
Taterillus arenarius	30	8	20	lM	–	Mauritania	–	(Matthey, 1969—as *T. nigeriae*, see Robbins, 1974)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
Taterillus congicus	54	12	40	ISM	–	C. African Republic	–	(Matthey and Petter, 1970)
	54	–	–	–	–	Chad	–	(Tranier *et al.*, 1974*a*)
	54	–	–	ISM	sSM	C. African Republic	–	(Genest and Petter, 1973)
	54	12	40	ISM	–	C. African Republic	R	(Benazzou *et al.*, 1984)
Taterillus emini	44	22	20	ISM	–	Ethiopia	–	(Matthey, 1969)
	44	–	–	–	–	C. African Republic	–	(Genest and Petter, 1973)
Taterillus gracilis	36,37	10	24	lM	SM,M	Senegal	–	(Matthey and Jotterand, 1972—Autosoml polymorphism in addition to XY1Y2 system)
	36,37	8	26	lM r	mSM,M	Burkina Faso	–	(Matthey and Petter, 1970)
	36	–	–	ISM	–	Senegal	–	(Viegas-Pequignot *et al.*, 1982)
	see also *T. pygargus*							
Taterillus harringtoni	44	20	22	ISM	mSM	Kenya	–	(Robbins, 1973)
Taterillus lacustris	28	18	8	ISM	mSM	Cameroon	–	(Tranier *et al.*, 1974)
Taterillus nigeriae	No data (see *T. arenarius*)							
Taterillus petteri	18,19	–	–	–	–	Burkina Faso	–	(Gautun *et al.*, 1985)
	18,19	16	0	–	–	Niger	–	(Tranier, 1974)
	18,19	16	0	–	–	Burkina Faso	R	(Benazzou *et al.*, 1984; Sicard *et al.*, 1988)
Taterillus pygargus	22,23	20	0	ISM	M,SM	Senegal	–	(Matthey, 1969; Matthey and Jotterand, 1972)
		(Autosomal polymorphism in addition to XY1Y2 system)						
	22,23	20	0	SM	SM,SM	Senegal	R	(Ratomponirina *et al.*, 1986)